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THE ANALOGOUS SHAPES OF CELLS AND BUBBLES

By Frederic T. Lewis

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Harvard Medical School, Boston, Massachusetts

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Introduction

In the slow movement toward presenting fundamental biological forms on a physical and mathematical basis, recent studies of cell shape play an important part. Among the forces which determine the forms of cells whether solitary or in contact with one another, Sir D'Arcy Thompson finds that "surface tension is certainly of great, and is probably of paramount importance."[1] But the surface tension of several types of simple cells has been measured and found very low—"of the order of 0.1 to 1.0 dyne per cm."[2] Indeed it is supplemented by other surface forces, viz. "an elastic tension which may be a function of the cell-membrane thickness, and an elastic tension in the cortical gel layer of the cell," so that Danielli, whom we quote, finds that "the solution of most of the problems of cell form is at least some way beyond our immediate grasp." The existence of cilia, which Professor Thompson regards as "*sui generis;* we know nothing of them from the physical side," leads Danielli to comment that they are "in frank contradiction to a belief in any kind of dominant role for surface tension forces."

Soap bubbles, solitary or in collocation, with which cells from earliest times have been compared, are conformed (according to

Thompson) by surface tension "in the absence (to all intents and purposes) of alien forces from the field." Matzke, who has provided unique and valuable data on the three-dimensional shape of soap bubbles in foam, dissents, asserting that "other forces such as adhesion and gravity are still present."[3] Instead of ascribing bubble shape to surface tension, he uses the more general term "surface forces" for the controlling factor. He finds that the bubbles are of such diverse shapes that although significant average numbers of facets can be demonstrated, "no one combination among those found could be considered the type"—"Kelvin's ideal figure is not achieved."[4]

So also, in the long and growing series of statistical studies of cell shape in unspecialized plant tissues, by Dr. Matzke or under his direction,[5] it is consistently held that "none of the combinations found was clearly predominant, and none is interpreted as 'the type'." His statistics are unquestionably accurate, and his preparations which fail to show the Kelvin pattern, fail also to show any substitute type. To conclude from such data that there is no type is to retreat from a position supposedly gained toward the mathematical and physical interpretation of cell forms. Before conceding the loss, it is here proposed to review the basis for accepting the Kelvin pattern as the typical shape both of bubbles and of cells. In regard to type cells, our point of view is precisely that of Jeffries Wyman in his "Notes on the Cells of the Bee" (1866). After enumerating eight "marked variations" in honeycomb, he comments:[6]

> In view of the frequency of such variations, however near the bee may come to a typical cell in the construction of its comb, it may be reasonably doubted whether a type cell is ever made. Here, as is so often the case elsewhere in nature, the type-form is an ideal one, and, with this, real forms seldom or never coincide. Even in crystallography, where the forms are essentially geometrical, we are told that 'natural crystals are always more or less distorted or imperfect,' and that 'the science of crystallography could never have been developed from observation alone.'

Typical Shape of the Initial Cell and Bubble

It is agreed that cells are primarily spherical. The human ovum, the yolk of a hen's egg, and the oösphere of the rockweed *Fucus* are familiar examples. Their form is due to the geometrical properties of space, and to surface forces tending to reduce their surface area to a minimum, both factors being indispensable and "paramount." If cubes had less surface per volume than spheres the initial cells would be cubical.

The property of liquids that causes them "to draw together into a shape which makes the surface area, and therefore the potential

energy, least for a given volume" is a form of molecular attraction known as surface tension.[7] But in all geometrical solids, considered as configurations of points in space, the internal points of the configuration in their relation to one another differ from those on the surface. Hence the mathematical contention that "the interior of a sphere is a solid, while the configuration consisting of that interior and the sphere, *i. e.* the sperical surface, is not a solid."[8] Similarly the internal molecules in a drop of pure water have been distinguished from those on the surface, which have a surface tension of 75 dynes per cm. In the initial cell, which for all its complexity is still a liquid drop, the outer layers, multiple and reinforced, become visible as a cell membrane. Ectoplasm is set off from endoplasm, ectoderm covers entoderm, as is inherent in a geometric solid.

The initial soap bubble is a liquid drop with a central cavity. The film that forms its wall is commonly described as composed of three layers, viz. an outer and an inner surface layer, simple or stratified (both being in contact with the air and hence similar in structure) between which there is a middle layer, more or less developed, having no free surface. Thus the bubble is comparable with a coelenterate or a blastodermic vesicle rather than with an ordinary single cell, for their walls also consist of three layers,—ectoderm, entoderm, and intervening mesoderm. Although in bubbles of glass the existence of special layers has been denied, the wall of a hollow sphere inherently tends toward tripartite subdivision.

By optical and electrical methods the thinnest soap-bubble film has been calculated to be not more than 60Å thick (.006 μ)—too thin for direct microscopic observation of its layers. At that thinness the soap film has been figured diagrammatically as composed of two monomolecular surface layers of normally oriented soap molecules, held together by intervening liquid.[9] An ordinary soap film is much thicker, and Perrin has described it as formed of many laminae or identical leaflets, superimposed like the layers in mica, making the thickness of the entire film at any point an integral multiple of that of the primary leaflet.[10] This does not provide a middle layer such as Willard Gibbs assumed in describing the contact between a vertical soap film and a horizontal plate of glass. He wrote:[11]

> At such an edge (where a soap film meets a glass plate at right angles) we generally find a liquid mass, continuous in phase with the interior of the film, which is bounded by concave surfaces, and in which pressure is therefore less than in the interior of the film. This liquid mass therefore exerts a strong suction upon the interior of the film, by which its thickness is rapidly reduced.

The layers in a contact of that sort can readily be detected with a hand lens, and may be prepared for study as follows. Using the soap solution recommended by Matzke[3]—triethanolamine oleate 7.5 g., glycerin 34 g., and distilled water 58.5 g.—and employing his method of blowing measured bubbles, a bubble containing 0.5 cc. of air may be brought into contact with a large cover-glass. It at once becomes detached from the nozzle of the syringe and forms a hemispherical bubble with no perceptible change in volume, attached to the glass by a "Gibbs ring." The cover and bubble can then be inverted and placed on the stage of the microscope, conveniently supported by a blackened block of wood, ½ inch thick, through which a 1-inch hole has been bored.

Under a 16-mm. objective the circle of attachment of the bubble to the under side of the cover-glass appears as a broad band subdivided into an outer, a middle, and an inner layer. A small portion of such a ring is shown at *o*, *m*, *i*, in Figure 1C. The middle layer is a light band containing particles in motion, being a portion of the "liquid mass continuous in phase with the interior of the film" (Gibbs). The wider outer and inner bands are flaring black expansions of the corresponding layers of the bubble film. The inner layer invisibly covers the glass within the hemispheric bubble, and the outer spreads upon the glass in the opposite direction. Perpendicular to the plane of the cover-glass, this Gibbs ring rapidly becomes thin and passes out of focus.

Certain optical reflections and diffractions complicate the picture. The light middle layer may appear split into several parallel strands. Both the outer and the inner dark layers regularly show a light line, usually toward their free margin, which differs in nature from the light middle layer. Since these light lines (photographed in Figure 1) vary from brilliance to extinction on rotating the preparation in reflected light, and shift their position with oblique illumination, they presumably are not structural laminae.

The Paired Bubble and Cluster of Three

When two equal spherical drops of water, or of soap solution, are brought together, they unite in a single spherical drop with a loss in surface area of 20.6 per cent. A similar union, initiated when two 3-layered bubbles come in contact, is checked when their outer surface layers have been reduced by 16 per cent. As inferred from what is seen in Gibbs rings, the process of partial fusion involves a disintegration of their outer layers, beginning at the initial point of contact, and spreading over the entire circular contact area. Within the

circle, molecules of the disorganized outer layers may be added to the liquid middle layer, but at its circumference the outer layer of one bubble maintains unbroken continuity with that of the other. Since the inner surface layers do not come in contact, they show no reduction. On the contrary they are stretched, and increase in area, presumably by incorporating molecules from the middle layer, until they have grown by approximately 5 per cent. When the area of the reduced outer layers is to that of the increased inner layers as 4 to 5, the bubbles come to rest in a characteristic pattern figured by Thompson,[1] ('42, p. 473), who discusses it geometrically as if the bubble walls were single layers. The pattern is that made by two circles of equal radius which overlap by half the length of the radius: the overlapping arcs are then replaced by their common chord which represents the septum.

A precisely similar pattern is formed by the Gibbs rings of two hemispherical bubbles of equal size, immediately upon coming into mutual contact when deposited on a glass plate. Figure 1A is a photograph of one end of the septum, vertically oriented, as it joins the convex bubble walls. It is seen that the septum has acquired the structure and thinness of the outer walls, and since all three exert equal tensions, they (or their tangents) meet at angles of 120°. The tension of the septum checks the coalescence of the bubbles when their net loss of surface is limited to 5.5 per cent.

When a third bubble of the same volume is brought into contact with the septate pair, it may form a straight or bent chain of three. If, however, it crosses or merely impinges upon the end of the septum between the pair, the group at once becomes a trefoil cluster, bounded (on the glass plate) by three semicircles of equal radius ($r = 1.0$). From the three points of junction of these semicircles, septa of equal length ($\sqrt{4/3}$) converge to a central vertex, meeting at angles of 120°. The axial structure which they form upon the glass is photographed in Figure 1B.

Thus the contact of a third bubble across the notch at the top of Figure 1A, and the consequent disintegration of the contiguous outer layers, has converted the outer bubble walls into septa, the two new ones being structurally identical with the first one, and under the same tension. At their distal ends they meet the tangents of the outer bubble walls at angles of 120°, duplicating the pattern of Figure 1A. A continuous outer layer invests the entire cluster, having a surface area 25.7 per cent less than those of three separate equal bubbles of the same total volume. The inner surface areas are increased by 6.7 per cent, so that the three bubbles in becoming a trefoil cluster

reduce their total surface by 9.5 per cent—4 per cent more than was accomplished by the pair, which accounts for their pattern. Tension of the septa prevents further reduction. The three spherical segments appear to be nearer three-quarters of an entire sphere (74.1%) than "approximately five-sevenths" as recorded by Dewar[12] and later, perhaps not independently, by Thompson.

The axial structure in the trefoil cluster is a triangular-prismatic space filled with soap solution, into which the liquid middle layer of the septal walls drains, as described by Gibbs. Such triangular spaces (triangular in cross section) are always found where three bubbles meet. They follow all the edges of the polyhedral bubbles throughout a foam; and since they are not rings, they have been called "edge canals." They drain the "interfacial spaces" occupied by the middle layer of the bubble walls, and in turn they empty into tetrahedral "corner cavities" where four bubbles meet. If the cluster of bubbles rests on a glass plate, the plate, against which the soap films flare, serve as the third bubble enclosing a canal, or a fourth one at a corner.

The same configuration is found in certain metal alloys, resulting "from an attempted approach to equilibrium between phase and grain interfaces whose surface tensions geometrically balance each other at the points and along the lines where they meet."[13] Not only are there "drawings of cells in both elder pith and human fat that a metallurgist would immediately accept as sketches of isolated metal grains," but liquid lead in relation with grains of copper may present the pattern of triangular-prismatic edge canals and tetrahedral corner cavities as described both for cells and for soap bubbles (see C. S. Smith,[13] fig. 18).

There are several features of the photographs (Fig. 1) which the writer is unable to explain. The edge canals become very slender before entering the corner cavities—so fine that they are difficult to detect and may sometimes be occluded. Within the *peripheral* corner cavities (Fig. 1A) the soap solution is generally gray, whereas in a *central* cavity (Fig. 1B), which is at the end of a vertical axial column of the solution, it is yellow. Yet it was unexpected that the contents of such cavities would photograph as black and white respectively, both in diffuse and polarized light. The cavities show a refractive lining; and tension in the curved liquid-crystalline films which form their walls produces a transverse line, with a more or less distinct marginal notch at either end, that bisects the wall of the cavity in a node-like manner. On either side of this "node" there is a pale nodule, perceptible in ordinary light though obscure in photographs, which becomes conspicuous in polarized light (Fig. 1D). Some of these features have striking cellular analogies.

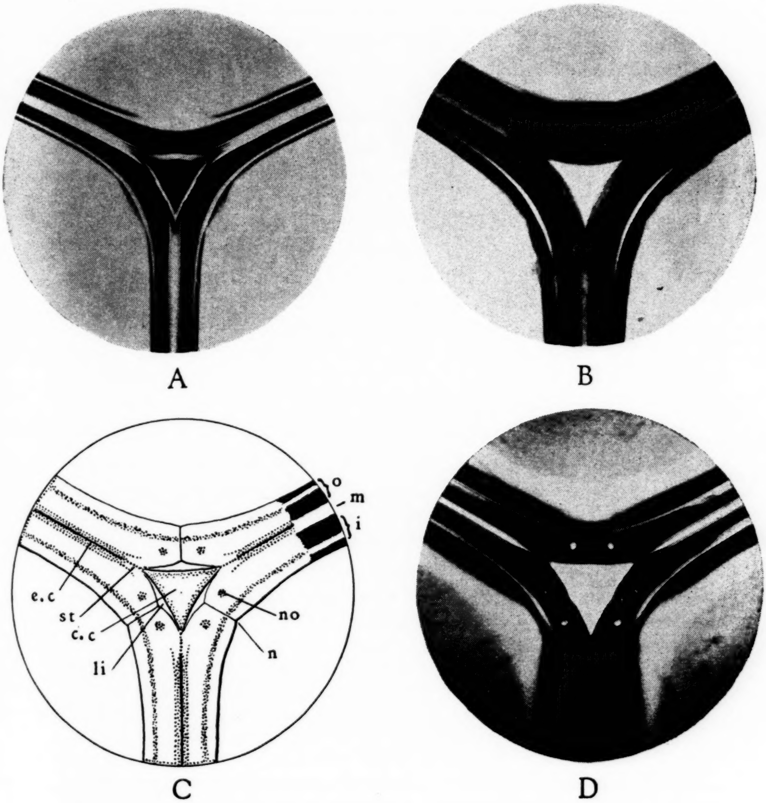


FIGURE 1. A. Portion of the walls of a conjoined pair of bubbles adherent to the under side of a cover glass, through which they were photographed. The triangular accumulation of soap solution is where the convexly horizontal walls of the pair join their vertical septum. B. Like A except that a 3rd bubble has come into contact with the horizontal arms of A, converting them into septa: the triangle is now the center of a trefoil cluster. C. Labels for photographs A, B, and D—*o*, *m*, and *i*, outer, middle, and inner layers of the bubble wall; *c. c*, corner cavity; *e. c*, edge canal; *li*, lining of corner cavity; *n*, node; *no*, nodule; *st*, strait, or slender connection of the edge canal with the corner cavity. D. Like B, but with polarized light and crossed Nicols. All photographs × 35.

The Paired Cell and Cluster of Three

Unlike liquid drops or paired bubbles which by coalescence or partial coalescence reduce their surface as a result of surface tension, the mammalium ovum segments into a pair of cells with increased surface. Cell division always increases the surface area, and with associated changes in cell shape it constitutes a third basic factor in the form of cells. If a spherical nucleus divides in halves into two spherical nuclei, the surface area is increased in the ratio of 1 to $\sqrt[3]{2}$ or by 25.99 per cent, but unless cell walls are formed we have only binucleate or multinucleate cells. If a spherical cell becomes bisected by a septum which provides a septal surface for each hemisphere, the increase in surface would be 50 per cent. This, however, is materially reduced through the concurrent effect of surface forces. Nevertheless, division differs radically from "the liberation of surface energy which takes place spontaneously whenever two droplets meet: to break one droplet into two, we have to supply energy from outside."[14]

Although Bütschli's tentative suggestion, in 1876, that after nuclear division an *increased* surface tension in the equatorial region causes the cell to divide[15] has been favorably received, Robertson[16] argued that for division there must be an equatorial *diminution* of surface tension. Both postulates are faulty, but the title of Robertson's paper—"Note on the Chemical Mechanics of Cell Division"—and the simple experiment which he described as follows, may prove highly significant:—

> If, now, a drop of olive oil which is not too large (about 2 to 3 mm. diameter) be floated on a layer of water, and a thread saturated in N/10 alkali (NaOH, KOH) be brought gently in contact with a diameter of the drop, the almost immediate effect is the division of the drop into two.

Various oils may be used. A drop of cottonseed oil spreads on the surface of water as a thin film. A second drop in the midst of the film forms an ellipsoid, and when a cotton thread soaked in a solution of caustic soda is applied to the ellipsoid, the drop breaks into two or more fragments, which shoot apart as if by mutual repulsion. Having come to rest as round droplets, some of the fragments may then reunite through surface tension. It has been said that during the division of the ovum, the two new parts tend to repel each other after the division is finished.[17] The disruptive force in this experiment is associated with the formation of soap, and Robertson, in 1909, thought it "possible that cholin, set free in nuclein synthesis, brings about in a similar manner, the division of the cell through the forma-

tion of soaps in the equatorial planes." Four years later he conceded that there was no valid evidence in support of that idea.[18]

The simplest cell membrane in animal cells is described as a fatty or oily layer—a lipoid-containing pellicle—invisible or scarcely visible with the microscope.[19] It soon undergoes a triple subdivision by the development of a middle layer of intercellular substance between the membranes of adjacent cells. In plants also, according to I. W. Bailey,[20] the cell wall is "actually a three-layered structure composed of two modified, cellulose-containing primary walls and a truly isotropic intercellular layer." In both animal and plants the middle layer is a product, formed between the cells, whereas in bubbles it is the formative material itself—the soap solution—which exists throughout the film that bounds the initial bubble.

The coherent pair of cells formed when the mammalian ovum divides in two differs from the conjoined pair of bubbles by having a deep notch between its halves. Studies of living ova by Warren Lewis and his associates have shown that this is not the compressing effect of the encapsulating zona pellucida. "The pressure of the zona may play a role, but a very minor one if any."[21] The notch between the cells is not crossed by a continuous outer film as in the bubbles photographed in Figure 1A. No such conjoining film is seen in photographs of the 2-cell stage of mice and rabbits, and none could be found in the corresponding preparations of the pig's ova, made by Dr. C. H. Heuser, which the writer was privileged to examine.[22]

Similarly the trefoil cluster of cells bears only a general resemblance to that of bubbles. It is a pattern duplicated by the agglutination of three egg yolks freed from the whites, which are in fact single food-laden cells. There is a triangular space between them as in Figure 1B, but it is larger and empty of cell substance: the tripartite adhesion walls are shorter, so that a greater portion of each sphere remains free. Yet the cell and bubble trefoils are comparable in their symmetry.

Euler's Theorem in Relation to the Paired and Trefoil Clusters

The famous and important proposition[23] that "in every solid bounded by plane surfaces the number of solid angles plus the number of surfaces exceeds the number of edges by 2," may freely be extended to an endless variety of biological shapes with surfaces variously curved. It applies to the pea-pod, whether it be considered as having 2 angles, 2 surfaces and 2 edges, or, as a folded leaf, it presents 2 angles, 1 surface and 1 edge. If indeed it were pendent and pyriform, with 1 angle, 1 surface, and no edges, the pervasive theorem would

still apply. The spherical ovum, lacking a meridian connecting two poles which would relate it to one of the pea-pod shapes, and unless it is considered a polyhedron with an infinite number of facets, is an exception. So also is the paired bubble unless the circumference of its circular interface be regarded either as uniangular, at some point having its beginning and end, or as a polygon having an infinite number of sides. The trefoil cluster, however, with no axial interspace, conforms both as a whole, and in its three segments separately: —all have 2 angles, 3 surfaces and 3 edges. In foams and tissues, all the many-faceted shapes assumed are subject to Euler's law.

Three Possible Arrangements of Four Cells

"This subject has hitherto been wholly neglected," Schleiden wrote in 1845, "though it must form the foundation of the whole science of morphology."[24] When four new cells arise, as he explained with a diagram, they may be either in a row linearly; or, two and two beside each other, they may spread in a plane; or one may be centered above a trefoil cluster composed of the other three, and initiate a solid. It will be a long time, Schleiden thought, before we can account satisfactorily for the production of these diverse arrangements, and it must suffice to have called attention to their "durchgreifende Wichtigkeit" ("paramount importance," in Lankester's translation). Cell shape is determined accordingly. In linear series, as in the stamen hairs of Tradescantia, the cells form filaments; in single layers, which are next to be considered, they produce membranes; and in superimposed layers or in masses, they yield parenchyma.

The Shape of Cells and Bubbles in Single Layers

Turpin[25] in 1829, groping toward the cell theory, pictured spherical vesicles arranged in a layer, as becoming hexagonal by mutual pressure, and as forming 14-hedra in masses. As cells, his 14-hedra are incorrect and unstackable, but there are significant features in his simple figure of the alga *Bichatia vesiculinosa*, Turpin (now *Gloeocapsa coracina*, Kützing) which he failed to record. In outline his drawing is reproduced as Figure 2A, showing 12 cells that form a single layer.

Such one-layered clusters, unless composed of few cells or those in a double row, consist of central cells and peripheral cells. The central cells have two free surfaces (above and below respectively) and a varying number of lateral contacts with those around them. Each free surface and lateral contact produces a polygonal facet whereby the sphere becomes a polyhedron. Peripheral cells or bubbles, if the single-layered cluster is suspended in fluid or floating in air, have only one free surface. Bubbles especially tend to be arranged in *compact*

clusters, so that, for example, when 4 are in contact with a 5th, the 4 will form a continuous row and will not occur isolated or divided into groups.

When a single layer of cells or bubbles is wholly free, and when, as with bubbles under Plateau's law, all vertices are 3-rayed and all corner-angles trihedral, the total number of facets (F) of all the cells or bubbles in a compact layer may be expressed in a simple formula. If nc is the number of central cells, and np the number of peripheral cells, then

$$F = 8nc + 5np - 6$$

The numerals placed in Figure 2A indicate the number of facets of the individual cells. In accordance with the formula, a layer of cells can not consist only of octahedral central and pentahedral peripheral cells, or of those averaging 8 and 5 facets respectively; there must be a few deviations to provide the deduction of 6 facets. In Figure 2A this is accomplished by 6 tetrahedral peripheral cells. The deviation, however, may occur partly or sometimes wholly in the central cells.

The total number of sides of the polygonal facets that cover a single free layer of bubbles or cells taken as a whole, above, below, and over its outer margin, is also regulated. Thus the layer in Figure 2A presents external facets of two shapes. The central cells are hexagonal above and below, and the apparent pentagons of the three pentahedral cells, when continued to the under side of the layer, are also found to be hexagons. The free surface of the six tetrahedral cells, when so continued, remains 4-sided. Every vertex in this group is 3-rayed. If four edges met at a vertex, it is readily seen that two adjacent polygons would each lose a side; 4 sides would be lost for every 5-rayed vertex, and so on. Then, if S is the number of sides of the polygons covering a layer, and n is the number of facets they enclose, with v_4 the number of 4-rayed vertices, v_5 the number of 5-rayed, etc.,

$$S = 6\,(n - 2) - 2v_4 - 4v_5 \text{ etc.}$$

Ordinarily 4-rayed vertices are infrequent, or, as in Figure 2A, altogether absent, and the formula then means merely that the polygons covering the layer have 12 fewer sides than if they were all hexagons. Its importance lies in the fact that it applies not only to the polygons covering layers and masses of cells, but also to those which cover individual cells, where tetrahedral angles form the 4-rayed vertices. In testing this formula by the peripheral cells in Figure 2A, it will be found that they all have two 2-sided facets, each bounded by an arc and its chord.

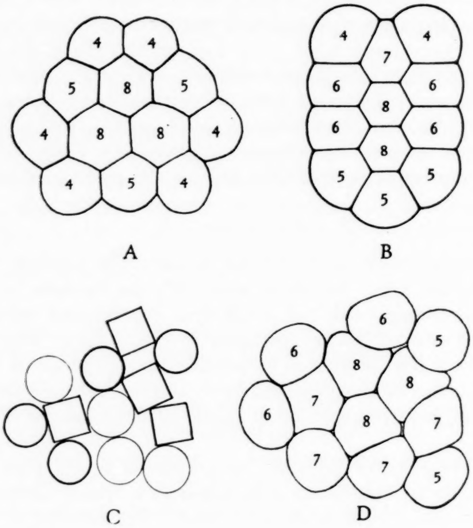


FIGURE 2. A. Single layer of 12 cells outlined from Turpin's drawing of Bichatia (1829). The numerals are the numbers of facets of the cells when the layer is free from a substratum. B. Layer of 12 bubbles (½ cc.) adherent to a glass plate. Photograph, to which the numbers of facets of the adherent bubbles have been added. C. Arrangement of 12 plasticine bodies of equal volume—cubes, cylinders and spheres—which on compression between 2 glass plates yielded the pattern D. The facets added to these bodies by both plates are included in the numerals in D.

The foregoing exacting requirements as to the number and shape of the facets presented by cells in a single free layer can be met by averages of very diverse forms, or by the prevalent occurrence of the few typical shapes. Thus if the 3 central 8-hedra in Figure 2A should divide in halves in the planes of apothems, the resulting layer of 15 cells might contain no central 8-hedron, but, with lowered average number of facets for the central cells, the entire layer would still comply with the formula. The same would be true if the peripheral cells divided, raising the average facets of the central cells, or if, as commonly happens, both kinds divide. Free layers composed of many cells thus maintain the general average of 8 facets for central cells and 5 facets for peripheral cells, with the required deduction of 6 facets per

layer. The 5-faceted form of the peripheral cell is that which would result from bisection of a central cell in the plane of an apothem and the merging of the division plane with the bisected top and basal facets in a single free surface.

In a layer of bubbles there is no division, and therefore the typical shapes may be freely presented. It is easy to make a compact layer of 100 bubbles with 60, or somewhat more, central bubbles all of the typical 8-hedral form—the only shape that can occur uniformly under the specified conditions.

Single layers of bubbles upon a glass plate present cell-like patterns, but with a precision rarely approached in cells (Fig. 2B). Against the glass every peripheral bubble adds a basal facet; whereas the number and shape of facets of the central bubbles remain unaltered. Hence the facet formula becomes $F = 8nc + 6np - 6$, as exemplified by the numerals in Figure 2B. The formula for the number of sides of the polygons covering the layer, $S = 6\,(n - 2) - 2v_4$, applies without change. In the cluster figured there are 10 peripheral bubbles with 10 4-rayed vertices, formed where any two adjacent free surfaces meet the two corresponding basal surfaces—all 4 at one point.

If the 13th bubble is added along the side of the cluster of 12 in Figure 2B, it promptly takes the 4-faceted form shown at the top of the photograph, quite like that of a member of an isolated trefoil group. Another bubble of the same volume placed beside it would cause it to become 5-faceted, like the three at the bottom of the figure. These in turn become 6- and 7-faceted through added contacts, the heptagonal bubbles being characteristically stretched out by retaining a narrow lateral connection with the film investing the entire cluster. When the lateral free surface is lost, usually by adding another bubble to the layer at that point, the peripheral bubble retracts as a central octahedron. Occasionally the adjacent tetrahedra meet across the top, converting the peripheral heptahedron into a central pentagonal prism, which remains heptahedral. Although a regular pentagonal prism of a certain height has less surface area per volume than any other plane-faced geometrical solid with 7 faces, the inclusion of a pentagonal bubble among the central hexagons necessarily increases the average surface area.

Of the plane-faced bodies of equal volume which can be mutually conjoined to form a single layer without interstices and which have single free surfaces above and below, hexagonal prisms, in height equal to the apothems of their terminal regular hexagons, present the least possible surface. When the volume of such a prism is 1.0, the length of the sides of the terminal hexagon is $\sqrt[3]{2/9}$ or .60571 and the area

of the hexagon is .95318; the height of the prism is 1.04912. The "surface index" of this minimal hexagonal prism, or its surface area divided by that of a sphere of equal volume is 1.1826.

The greater surface of the minimal pentagonal prism of equal volume (nearly 1.6 per cent) is indicated by its index 1.2015. It does not at all fit into a mosaic of minimal hexagonal prisms since its sides are longer, the area of its terminal polygon is greater, and its height is shorter than that of the hexagonal type (Table I). It can

TABLE I

Regular Right Prisms of Equal Volume ($V = 1.0$) and Least Surface

End Polygons			Height of Prism	Surface Index S/Σ
Number of Sides	Length of Sides	Area of Polygon		
4	1.0000	1.0000	1.0000	1.2407
5	.7502	.9684	1.0326	1.2015
6	.6057	.9532	1.0491	1.1826
7	.5098	.9446	1.0587	1.1719
8	.4410	.9392	1.0648	1.1653

be incorporated in the layer of hexagonal prisms only by deviations which further increase its surface, or that of the adjacent prisms, in varying proportions.

It is necessary, however, from our corollary of Euler's theorem, that with the pentagonal bubbles an equal number of heptagonal forms be introduced, provided that the central bubbles are limited to these 3 shapes and that the added facets are not, wholly or in part, relegated to the peripheral layer. The minimal heptagonal prism, with an index of 1.1719, has 0.9 per cent less surface area than the minimal hexagonal prisms of the same volume. For voulme 1.0, the sides of the heptagon are shorter than those of the hexagon; its area is less; and the height of the prism is consequently greater. The diminished surface area of this minimal heptagonal prism would be partly offset by the deviations required to fit it with other bubbles in the layer, but even if it could be fully retained, the introduction of a minimal pentagonal prism matched by a minimal heptagonal prism would cause a net increase in surface area over that of 2 minimal hexagonal prisms of 0.35 per cent.

A similar increase in area would result from including minimal prismatic bubbles of more than 7 sides, although their own areas

diminish with every added side. Thus the presence of a minimal octagonal prism, with 1.46 per cent less surface than the minimal hexagonal prism of the same volume, would cause a net addition to the surface area, whether balanced by a minimal quadrilateral prism (a cube) or by 2 pentagonal prisms. Bubbles may readily be induced to depart from their typical minimal shapes and to come to rest in diverse irregular patterns of greater surface, which they maintain with considerable stability.

Unexpectedly it is found easier to produce a central pentagonal bubble with its increased surface than to form a central heptagonal bubble with decreased surface. This may be because the pentagonal prism of a certain height has the least possible surface for a 7 plane-faced polyhedron, whereas the heptagonal prism is not the form with least surface for the 9-faced. If, however, a cluster of 19 bubbles of equal volume is made upon a glass plate, consisting of a central bubble surrounded by an inner circuit of 6, and enclosed by an outer circuit of 12 (an arrangement shown by the heavily outlined bubbles in Figure 4), and if then the central bubble is broken, the entire cluster immediately readjusts itself and fills the gap. The remaining 6 central bubbles frequently form 2 pentagonal, 2 hexagonal and 2 heptagonal prisms, or sometimes 3 pentagonal and 3 heptagonal, the perimeters and areas of which may be measured in photographs similar to Figure 2B.

It is found that the hexagonal prisms have become irregular, with longer sides against the pentagonal prisms and shorter sides against the heptagonal, as would be expected from Table I. Although the average length of side of the pentagonal bubble is greater than that of the hexagonal, which in turn is greater than that of the heptagonal, the differences shown in the table have been reduced so that the relative areas of the polygons have been reversed. The average areas of the central polygons are found to vary directly with their number of sides.

In explanation it may be said that the sides or septa of the bubbles, being alike in structure and in tension, tend to meet at angles of 120°, for only at that angle can each septum be the equilibrant of the other two and all equilibrants equal. Hence the central bubbles tend to become regular hexagons in cross section, with an area determined by 6 equal contractile forces acting upon the contained air. When pentagonal in section, with average internal angles of 108°, the resultant contractile tensions of the 5 septa forming the pentagon exceed the stretching force of the 5 septa attached to its exterior, and the cross-sectional area becomes smaller. In heptagonal bubbles, with

average internal angles of 128°, the stretching tension exceeds the contracting, and the 7-sided bubbles are larger in section than the 6-sided. But in the peripheral bubbles all internal angles approach 120°—the contractile force is proportional to their number—and their areas of contact with the glass vary inversely with their number of sides (Fig. 2B).

An important feature of the prismatic central bubbles conjoined in a single layer is the dome with which each of them is capped. If this dome were a portion of the sphere within which the corresponding minimal flat-faced hexagonal prism is inscribed, the conditions outlined in Figure 3 could result. Figure 3A represents the cross section of the upper end of the hexagonal shaft of the domed prism within a small circle of the circumscribing sphere, at the level *c-d* of Figure 3B.

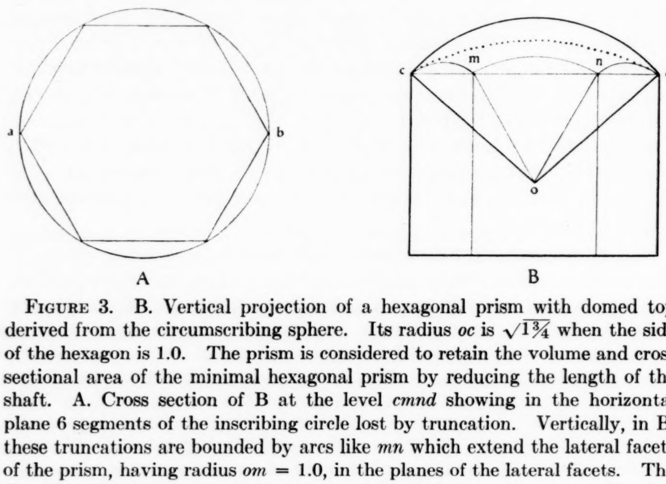


FIGURE 3. B. Vertical projection of a hexagonal prism with domed top derived from the circumscribing sphere. Its radius *oc* is $\sqrt{1\frac{3}{4}}$ when the side of the hexagon is 1.0. The prism is considered to retain the volume and cross sectional area of the minimal hexagonal prism by reducing the length of the shaft. A. Cross section of B at the level *cmnd* showing in the horizontal plane 6 segments of the inscribing circle lost by truncation. Vertically, in B, these truncations are bounded by arcs like *mn* which extend the lateral facets of the prism, having radius *om* = 1.0, in the planes of the lateral facets. The dotted arc *cd* shows the height of a cap derived from a sphere of radius 2.0, subtended by a central angle of 60°.

Figure 3B is a vertical projection of that prism with its dome derived from the circumscribing sphere, being a portion of the spherical segment of one base subtended by a central angle, *c o d*, of 98° 12′ 47″.

The domed prism in 3B, as a central bubble resting on glass, would have less surface area than the form which bubbles actually assume, but it is incompatible with an equal tension in the vertical walls and the tangents of the dome. Consequently, with increased surface, the

curve of the dome is reduced to that of a spherical segment subtended by a cone with apical angle of 60°. The radius of the sphere which provides the rounded cap is then twice the length of the sides of the hexagon. If the vertical circular segments remain as before (i. e. like the arc *m-n* in Fig. 3B) the tangents of all three domes which meet at a vertex in the hexagonal mosaic would form angles of 120° with the vertical edges of the prism. I am indebted to Mr. William A. Pierce for suggesting this combination, which is tentatively presented as the typical shape of central bubbles in a single layer when resting on a glass plate. The free surface is no longer a portion of a simple spherical segment, but is a modification, the area of which has not yet been determined.

Epidermal cells resting on a basement membrane may present comparable forms. Over the tall prismatic cells in the cucumber, low domes have been found, appearing like segments from spheres of radius 3.86 times the length of the hexagonal side, thus being subtended by cones of 30°. From calculations made by Graustein[26] it may be reckoned that such a low dome would reduce the surface index of a minimal hexagonal cell from 1.1826 to 1.1606. Higher domes would reduce it more, but tension appears to check this reduction when the subtending angles are 60°.

The Shape of Solids Compressed in a Single Layer

"There is no doubt but that solids possess surface energy and that the only reason that this does not manifest itself more clearly as a surface tension is that solids do not possess sufficient mobility."[27] Matzke,[3] conceding that surface forces are "of relatively greater importance in the bubbles" than in lead shot—that they are "more effectively significant in the soap film system than in the lead shot system"—does not exclude them altogether from a share in shaping compressed solids. Yet the deformation of plastic solids by an external force, whereby their surface area is increased, contravenes the effect of whatever surface tensions such bodies possess. Radical differences in the resulting forms may therefore be expected.

Twelve plasticine cubes of different colors were made with ½ inch edges; four of them were rolled into spherical form, and four into cylinders ½ inch tall, all being therefore of the same volume. They were placed haphazard on a glass plate, except that they were near enough together so that each was in contact with at least one other (Fig. 2C). A glass plate was placed over them, and in a screw press the distance between the parallel plates was reduced to ¼ inch.

During compression the cubes lost the sharpness of their peripheral angles which were disregarded in counting the facets for Figure 2D.

The interfacial layer of air, corresponding somewhat with intercellular substance, is pressed out from between the plasticine surfaces which, except for color differences, would blend indistinguishably. Several triangular edge canals are seen in Figure 2D, and two quadrilateral spaces. Another turn of the press would reduce the canals to 3-rayed vertices, and the quadrilateral spaces would become small facets in the direction of their long axes. In numbering the facets in the figure, these spaces have been considered as already eliminated. Pressure from the glass plate above and below provides, or preserves, a top and basal facet for all the plasticine bodies, and assuming that any 4-rayed vertex appearing in Figure 2D extends from the top to the basal surface, the formula now becomes

$$F = 8nc + 7np - 6 - 2v_4$$

The same formula would apply to the layer of bubbles if it were in contact with plates both above and below. Compliance does not depend on the uniform size of the bodies. If, for example, around the central octahedral body in Figure 2D the quadrilateral and the four triangular spaces should be occupied by very small cells, 6- and 5-faceted respectively, thereby adding facets to the surrounding bodies, the formula would still apply.

Features of the layer of plasticine bodies incompatible with dominant surface tension are (1) the existence of angles and edges over the free surface; (2) the frequent approach to 4-rayed vertices and their occasional formation (apart from those at the peripheral contacts with the glass plate); and (3) the marked irregularity of the polygonal areas in the central mosaic. Yet the layer of space-filling compressed solids is necessarily divided into central and peripheral bodies governed by the same formula for the number of facets as the layer of bubbles. This compliance depends on the prevalence of trihedral corners and 3-rayed vertices in both cases. In a free layer of bubbles vertices with more than 3 rays are eliminated by surface tension. For compressed solids the chances are heavily against the meeting of 4 or more compressed or enlarging bodies at a mathematical point.

The Shape of Bubbles in a Double Layer

The double layer of hexagonal cells in honeycomb which vegetable cells resemble sufficiently to account for their name *cells,* is readily seen to present a very different pattern from that of a double layer of bubbles. The typical cell in honeycomb is closed below by 3 rhombic facets, yet Müllenhoff[28] ventured to consider the work of the bees as a surface tension effect upon fluid wax! Vogt[29] refuted this

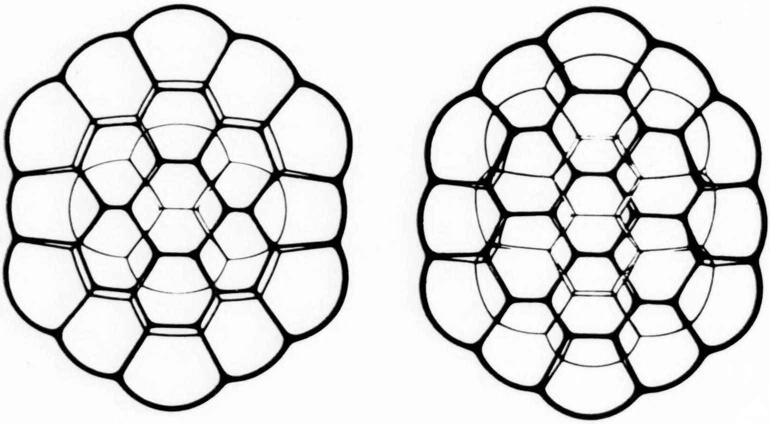
sufficiently; but Thompson reaffirms his belief that "we have to do with a true tension effect . . . in the first few cells of a wasp's comb we recognize the identical configurations exhibited . . . by a group of 3 or 4 soap bubbles." Soap bubbles in double layers never assume the form of cells in honeycomb, which have tetrahedral angles contrary to Plateau's law; nor do bee's cells provide the least possible surface for their volume. The saving in wax by a 4-faceted base of the bubble type, though definite, would be trivial, as verified by preliminary calculations for which the writer is indebted to Dr. R. F. Arens. So slight is the advantage in the perfect form that *bubbles* commonly depart from it.

When a fourth bubble is placed on top of a trefoil cluster, it becomes centered over the axial depression and acquires a 3-faceted base. If, however, the bubble is deposited over any similar 3-rayed vertex on the upper surface of a single layer of bubbles of equal volume, it does not remain there, but spreads to cover two vertices, or often three. Its base becomes 4- or 5-faceted. Further additions which develop a top layer produce a sheet of upper bubbles in which those surrounded by others will show, as found by Matzke,[3] "normally one hexagonal face above, in addition to 6 lateral contacts and 4 basal ones." That defines their type.

There is only one pattern of that description which can occur throughout both strata of a double layer (except at their periphery). Its production requires an orderly arrangement of the bubbles which is not produced by "blowing air through a soap solution" (Desch[30]), or by heaping bubbles of uniform volume in a cylindrical dish until they fill it, which was Matzke's better method. Over the floor of the chosen dish, bubbles of uniform volume, but varying in number, may form a continuous single layer, in which every peripheral bubble has a basal and a vertical facet against the glass and a free upper surface. Thus the total number of facets of the bubbles in that layer (as with the plasticine bodies) is $8nc + 7np - 6$. A bubble placed upon it to start a second layer is liable to be drawn down to the glass and added to the basal layer, sometimes as a quadrilateral bubble balanced by two adjacent heptagons, which cannot reduce the combined surface area (cf. Table I). Some pentagonal and heptagonal bubbles are sure to be introduced, and yet there will be a basal layer complying with the foregoing formula. In a dish full of bubbles, as seen in Matzke's photograph, the horizontal stratification and the orientation established by the basal layer tend to be preserved throughout the mass.

To avoid the effects of adhesion to the sides of the dish, 19 bubbles ($\frac{1}{2}$ cc.) were deposited in a compact cluster on a glass plate, and 4

bubbles of the same volume were placed above them in a second layer. In the photograph, Figure 4A, these upper bubbles are sharply but thinly outlined against the heavy edge canals of those below. Each of these bubbles has 4 basal facets exactly matched by upper facets in the basal layer. The heavily outlined central bubble of the basal group has acquired the typical shape which all but the peripheral bubbles in a duplex layer could exhibit uniformly. It is still a hexagonal prism, but 2 quadrilateral and 2 hexagonal facets have replaced the former upper surface, converting the octahedron into an 11-hedron.



A B

FIGURE 4. A. Cluster of 4 bubbles, lightly outlined, all with 4-faceted bases, resting on a basal layer of 19. The central basal bubble is a typical 11-hedron of formula 4Q–4P–3H. B. Six bubbles have been added to the upper layer in A: the 2 central upper, and 3 of the central lower, are typical 11-hedra.—Unretouched photographs of ½ cc. bubbles, × 1¼.

Two of the 6 lateral facets of the prism, opposite each other, have remained quardilateral, and the other four have become pentagonal. The eleventh facet is the hexagon against the glass plate. As a whole this bubble, having 4 quadrilateral, 4 pentagonal and 3 hexagonal facets (formula 4–4–3) has the pattern of a bisected Kelvin 14-hedron.

Before the overlying bubbles were deposited, the outline of the central basal bubble was a *regular* hexagon (as in Fig. 2B). Now it shows an interesting approximation to the irregular hexagon characteristic of certain bisections of Kelvin's orthic tetrakaidecahedron,

described by Grautsein and Matzke[31] as having two short sides of length a, four long sides of length $\sqrt{3}\,a$, internal angles between two long sides of 109° 28′ 16″, and between a long and a short side of 125° 15′ 52″, with an area of $4\sqrt{2}\,a^2$.

In Figure 4B six bubbles have been added to the upper layer in A, making two more typical 11-hedra in the lower layer, and two in the upper. Further additions in linear series could increase their number indefinitely, yet it seldom happens. As seen in Figure 5A–D, in which a lower layer of 10 bubbles presents 10 vertices to be covered by an upper layer, the production of the Kelvin pattern is not readily accomplished. It requires an upper layer of 7 bubbles (Fig. 5A) to cover the 10 vertices, and 4 upper bubbles must temporarily remain with 3 basal facets. Much more often the successively added bubbles

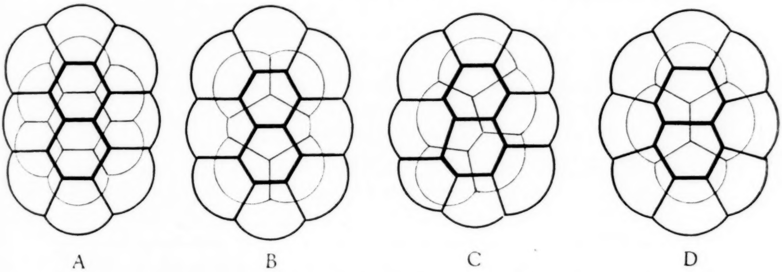


FIGURE 5. A–D. Four observed arrangements of bubbles in an upper layer placed upon a uniform basal layer of 10 bubbles, with 10 corners to be covered. Drawings (not photographs).

acquire at once a 4-faceted base (Fig. 5C), sometimes 5-faceted (Fig. 5D), with great consequent irregularity. Frequently (Fig. 5B, C, D) the basal bubbles end above in 3 pentagonal facets.

Furthermore, since a regular basal layer provides only 2 vertices apiece for similar bubbles of equal volume in an upper layer, the appropriation of 3 vertices by certain early arrivals there either reduces the number of overlying bubbles which cover all the vertices (Fig. 5D), or forces some of the upper bubbles to form 3-faceted bases. An upper bubble with a base of 3 pentagonal facets (not shown in Fig. 5) would be like the 2 central basal bubbles in 5B, merely overturned. They form less readily in the upper layer, where the bubbles glide freely over those below, than in the lower layer attached to the glass. Since it is a shape which cannot occur uniformly throughout a layer, occasional 10-hedral bubbles of that sort may be regarded as deviations from the 11-hedral type.

The Shape of Bubbles in Multiple Layers

On attempting to start a third layer by placing a bubble over the center of the upper layer in Figure 4B, the additional bubble generally wedges its way down into the second layer which it helps to make irregular. Confining the lower layers within a cylindrical dish does not prevent this result. The bottom of a circular dish 46 mm. in diameter may be completely covered by 19 bubbles (½ cc.) arranged like the basal layer in Figure 4. Five more bubbles placed upon it may be drawn down into that layer as would never happen with vegetable cells, in which gliding movements are so generally denied. Upon this variable foundation second and third layers are deposited,

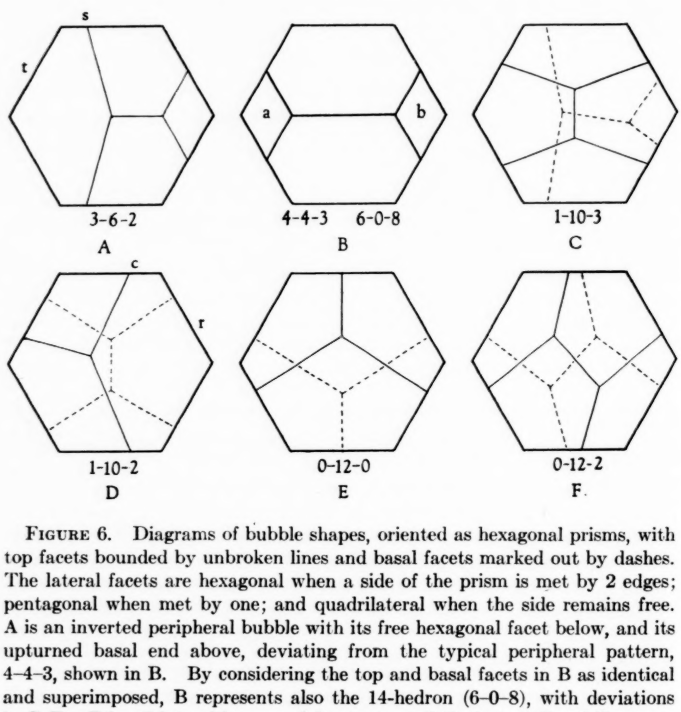


Figure 6. Diagrams of bubble shapes, oriented as hexagonal prisms, with top facets bounded by unbroken lines and basal facets marked out by dashes. The lateral facets are hexagonal when a side of the prism is met by 2 edges; pentagonal when met by one; and quadrilateral when the side remains free. A is an inverted peripheral bubble with its free hexagonal facet below, and its upturned basal end above, deviating from the typical peripheral pattern, 4–4–3, shown in B. By considering the top and basal facets in B as identical and superimposed, B represents also the 14-hedron (6–0–8), with deviations in C–F. F has 2 lateral hexagonal facets, toward the letters C and F respectively: bisection of one of them along an apothem yields the 0–12–3 combination:—of both, the 0–12–4.

also varying in their number of bubbles, with consequent inevitable irregularity. Very skillfully and thoroughly these forms have been pictured by Matzke,[3] both for peripheral bubbles, 400 of which had an average of 10.99 facets, and for central bubbles, where, for 600, he reported an average of 13.7 facets. No complete layer was tabulated, which from his photographed figure 1 would include approximately 150 bubbles. Two circuits "at least" of bubbles immediately beneath the peripheral layer were excluded from his tabulation.

The relation of the shapes which Matzke found most often to Kelvin's mathematical pattern is summarized in the diagram, Figure 6. The peripheral bubble, whether at the top of the full jar or on the sides against the glass, is expected to be the bisected 14-hedral form already described. It has 11 facets (Fig. 6B), its free surface being hexagonal, its lateral surfaces quadrilateral (two of them) and pentagonal (the other 4), and its 4-faceted base combining 2 hexagons and 2 quadrilaterals. The total facets of each polygonal shape, in the order of their number of sides beginning with the smallest, make convenient formulas for such patterns, and for this peripheral bubble it is 4–4–3. Matzke found 22 examples in 400.

In what may be regarded as a deviation, one of the basal quadrilateral facets may be enlarged at the expense of the hexagons. Facet *a* of Figure 6B could thus become the basal hegaxon of Figure 6A, or in a lesser deviation the septum *s* might terminate at *t*. The different patterns which result are both within the formula 3–6–2. Since either the quadrilateral *a* or *b* of Figure 6B may be the one to enlarge, and either its upper or its lower side may be the one to remain relatively fixed, the resulting combinations of facets occur in inverted and mirror image forms. Including all its varieties Matzke found 3–6–2 "the commonest of the 43 combinations of facets"—67 of them in 400 peripheral bubbles. The 11-hedral bubble in the basal layer of Figure 5C is an example of this shape in a setting which illustrates its origin.

Just as the bisected Kelvin 14-hedron is the expected form for the peripheral bubble, in which it is frequently realized and where its number of facets is the average actually found, the entire Kelvin 14-hedron is expected for the central bubbles, with an average of 14 facets for the deviations. The slight requisite deduction of 12 facets per layer, $F = 14nc + 11np - 12$, which may be either in the peripheral or the central bubbles,[32] could hardly be recognized in statistical studies of bubbles taken at random from the deep part of layers of many members. For 600 central bubbles Matzke[3] reports an average of 13.7 facets and finds that "the deviation from 14 is apparently not

without meaning." Of the Kelvin 14-hedral pattern "with 8 hexagonal and 6 quadrilateral facets" he saw "not a single one." What he has recorded in his unique and important study may be summarized as follows.

For the Kelvin 14-hedron the diagram Figure 6B serves without change, since its lower and upper facets, in this orientation, duplicate one another and may be considered superimposed. It has no pentagonal facets, and its formula is 6–0–8. If on its upper surface the quadrilateral facets *a* and *b* should enlarge until they met in a common vertical edge, a top of 4 pentagonal facets would result. Such a top over a base produced as in Figure 6A would make the irregular bubble 1–10–3 (Fig. 6C). With 73 examples in 600, Matzke found this the most common form of 14-hedral bubbles. A top of 4 pentagons may be produced on the central hexagonal bubble in a cluster of 7 by adding an upper layer of 4 bubbles in opposite pairs, 2 with 4-faceted bases and 2 with 3-faceted. One pair of the upper bubbles will form a common septum over the central bubble beneath. When, as in Figure 4A, that septum overlies a maximum diameter of the basal hexagon, the typical pattern results; but *over an apothem* it produces 4 pentagons.

A 4-faceted end above or below with a 3-faceted opposite end, often arising in the confusion of securing 4-faceted bases by unoriented bubbles (cf. Fig. 5), accounts for several forms with 13 facets which are included in Matzke's tabulation:—4–4–5 (4 bubbles); 3–6–4 (36 bubbles); 2–8–3 (19 bubbles); and 1–10–2 (Fig. 6D), by far the commonest arrangement of all, 118 examples. Its irregular 3-faceted top would arise if facet *b* (Fig. 6B) had enlarged to a hexagon and facet *a* been forced out of the picture. Another pattern of the 1–10–2 combination occurs when the edge *c* (Fig. 6D) is moved to *r*. The 3-faceted and 4-faceted ends may then become quite symmetrical.

When regular 3-faceted ends occur at both ends of a central hexagonal bubble, their pentagonal facets may be superimposed forming a 3–6–3 combination, or they may alternate (Fig. 6E) forming a more or less regular dodecahedron. In a haphazard distribution the 3–6–3 form should occur with the greater frequency, but it is indeed significant that Matzke found 50 pentagonal 12-hedra for 7 of the 3–6–3 pattern.

Of special importance is the 0–12–2 combination (Fig. 6F) produced by terminations of 4 pentagonal facets each, alternately oriented. If superimposed, these ends form one of the common 2–8–4 patterns (64 examples). Alternately oriented, and with all facets regular,

ERRATUM

In the Proceedings, Vol. 77, No. 5, p. 173, Table II, under "QPH" in column 5, for 0–21–1 read 0–12–1.

they yield, as Goldberg demonstrated, a polyhedron with less surface area than any other plane-faced 14-hedron of equal volume.

In a mathematical paper of great biological interest[33] Goldberg has shown that for convex polyhedra of the least surface for their volume—i. e., for the "best" polyhedra—pentagonal facets are introduced with the 7-hedron which has 2; and that their number of pentagons increases by 2 with every added facet up to the 12-hedron with 12, beyond which the number of effective pentagons cannot be increased. With Steinitz, Goldberg defines "the number $K = S^3/V^2$ where S is the surface area and V the volume of the polyhedron: then the 'best' polyhedra are those which have the smallest value of K." He finds that K for the pentagonal dodecahedron is 149.87; for the orthic 14-hedron of the same volume, 150.12: and for the 14-hedron (0–12–2) "formed by truncating the two apices of a double skew pyramid," 143.94. Matzke counted 39 bubbles of that last combination in 600.

How greatly the bubble shapes differ from those of cells is shown in Table II, derived from Matzke's statistics. It records the number

TABLE II

NUMBERS OF POLYHEDRAL BUBBLES IN 600, COMPRESSED SHOT IN 624, AND CELLS IN 550, HAVING EITHER 10 OR 12 PENTAGONAL FACETS. COMPILED FROM MATZKE'S DATA

Q P H	Bubbles	Shot	Cells	Q P H	Bubbles	Shot	Cells
1–10–6	0	0	0	0–12–4	10	0	0
1–10–5	4	0	0	0–12–3	21	1	0
1–10–4	35	3	1	0–12–2	39	2	0
1–10–3	73	3	1	0–21–1	—	–	–
1–10–2	118	5	1	0–12–0	50	3	0

of bubbles in 600, of compressed shot in 624, and of undifferentiated vegetable cells in 550, having the number of quadrilateral, pentagonal, and hexagonal facets listed in the columns Q, P, and H, respectively. The combination 0–12–1 is geometrically impossible. The division of one of the lateral hexagons in Figure 6F, along an apothem, into a pair of pentagons can occur by its coming in contact with 2 bubbles, each covering 3 vertices. This would convert the 0–12–2 combination into 0–12–3, and such a division involving both lateral hexagons of the 0–12–2 would produce the 0–12–4 pattern. In geometrically perfect form the K of that 16-hedron becomes 139.2 (Goldberg).

None of the bubble shapes with less surface than the Kelvin 14-hedron can be stacked uniformly to fill space. They must occur in a

variety of approximations, all of them involving an increase in their own surface area, and preventing the most effective reduction possible in the uniform Kelvin layer. It has not been shown that through irregularity anything "better" has been accomplished *for the mass as a whole,* than by regularity and the mathematical solution. On the contrary it is found that in the single layer of hexagonal prismatic bubbles, stable deviations from the type are frequent, and they involve an increase in surface. In a most careful study of the volumes and surface areas of *models* of 100 plant cells—a method which may be inadequate for such slight differences as would be presented—Marvin[34] has published data which fail to show a reduction in surface area proportional to the number of pentagonal facets, although such a reduction is quite possible. His figures indicate that the irregular cells average 4 per cent more surface than orthic 14-hedra of the same volume when compared cell by cell.

The average of 13.70 facets for the central bubbles, described by Matzke as "close to 14 faces," is not as close as may actually occur in entire layers. The typical central bubble is certainly not a 13-hedron —much less a regular dodecahedron—but a geometrical form which, under the dominant surface tension of bubbles, is subject to a series of deviations which Matzke has been the first to tabulate.

The Typical Shape of Undifferentiated Cells in Masses and in Surface Layers

From Matzke's data it is seen that a bubble within foam has an average of 9.17 pentagonal facets. This contrasts with compressed shot in which, as shown by Marvin, the average shot has 5.48 pentagonal facets. Undifferentiated cells resemble the shot, with an average of 5.32 pentagonal facets per cell. That does not differ appreciably from the number produced by truncating the 6 tetrahedral angles of a rhombic dodecahedron in all possible combinations of 3 planes at right angles: 729 polyhedra result, with an average of precisely 14 facets, and an average of $5\frac{1}{3}$ pentagonal facets per polyhedron.[35] These figures are sufficient to show that although bubbles with their paramount surface tension have a large excess of pentagonal facets, such facets occur commonly in all space-filling masses of polyhedra unless specially arranged to prevent them. Since no single form of polyhedron with pentagonal facets can uniformly fill space, either these bodies—bubbles, compressed shot, and cells—have no typical shape, as concluded from the Columbia studies, or the pentagonal facets occur in deviations from, or approximations toward, some typical shape which is geometrically possible.

There are two geometrical shapes which uniformly fill space without interstices and can provide hexagonal cross sections comparable with those in Figure 2. With 6 lateral surfaces in both cases, there may be 3 facets above and below (with edges from the central apex to *alternate angles* of the hexagon) forming rhombic 12-hedra; or there may be 4 facets above and below, as already described, forming orthic 14-hedra, with 58/100 of 1 per cent less surface than the 12-hedra. Misled by Buffon's experiment with peas and by the form of honeycomb, Kieser, in 1815, declared that as determined both by mathematical laws and by observation, the basic form of cells "must be" the rhombic dodecahedron.[36] That the basic shape is Kelvin's minimal tetrakaidecahedron is shown by the following considerations.

The average number of facets of central cells is found to be close to 14. In 7 simple tissues studied by 5 investigators, Matzke tabulates the average for 700 cells as 13.86 facets. By including 100 cells which have been reported by the writer and 200 later recorded by Hulbary, the average for 1000 cells becomes 13.95. There are several sources of error, so that this result is not inconsistent with an average of 14 facets for central cells. A slight downward deviation is expected from the occasional occurrence of tetrahedral angles, and may well be present from other causes, but the data leave no doubt that the average central cell is a 14-hedron.

The average number of facets of peripheral or epidermal cells, when in relation with underlying cells of the same diameter should therefore approach 11, with the bisected 14-hedron, of formula 4–4–3 as the type (Fig. 7). Realization of this shape depends on finding epidermal cells of the same average area in cross section as the cells underneath. Usually the subepidermal cells are larger, as in the two plant tissues first selected. In the cucumber, tall prismatic epidermal cells stand upon supporting cells measuring approximately 3 times their area in cross section, the cells in both layers presenting more or less regular hexagonal outlines. Consequently the geometrical pattern which such epidermal cells approach consists of 10-faceted and 8-faceted cells in the proportion of 2 to 1, reducing the average number of facets of the epidermal cells from 11 to 9⅓ (Lewis[37]). The very different epidermis covering Tradescantia stems consists of rod-shaped cells, 12 times as long as they are wide, placed lengthwise of the stem. They rest on cells of the same width and general shape, but 3 times as long. The epidermal pattern here differs from that in the cucumber by consisting of 10-faceted and *9-faceted* cells in the proportion of 2 to 1, making the average facets 9⅔ (Lewis[38]). It was noted, however, that with supporting cells twice the length of the epidermal (and

hence of twice their area in section) the latter would average 3 basal facets instead of 4. Thus they would average 10 facets instead of 11; their typical formula would be 4–4–2.

Matzke recently reported[39] that in Anacharis "the average number of facets for 200 epidermal cells was 10.005," and that the "commonest combination (4–4–2) was found in 34 cells." The subepidermal cells

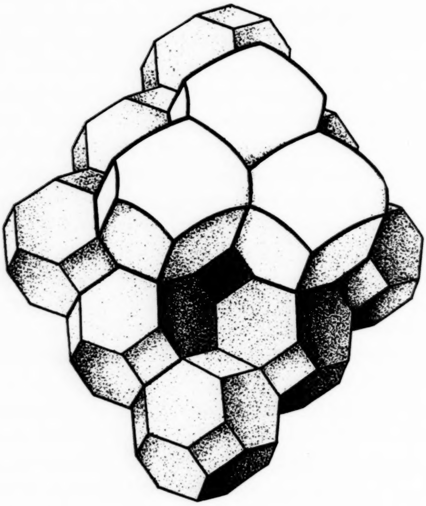


FIGURE 7. Three conventional epidermal polyhedra (4–4–3) resting upon a group of orthic 14-hedra (6–0–8), all of which are in prosenchymal orientation. The 14-hedra in this model, in parenchymal position, have been figured as typical of the cells in elder pith (Proc. Amer. Acad., 1923, 58, p. 554, Pl. I).

were described as "somewhat larger than those of the epidermis." The fact that the observations are consistent with a typical epidermis resting upon cells of twice their sectional area was not stated. Previously, after sampling a large number of living plants, Matzke had found epidermal and subepidermal cells "of approximately similar dimensions" in *Aloe aristata*. In the epidermis of its leaves he reported[5] that 200 cells had an average of 10.88 facets: 23 of them were of the pattern 4–4–3 (Fig. 6B), exceeded only by 34 of the 3–6–2 deviations (Fig. 6A). The foregoing observations all lead to the conclusion that the basic form of a simple epidermal cell is the 11-hedral bisection of a Kelvin 14-hedron.

A typical shape of vegetable cells is needed to explain their contrasting orientation in parenchyma and prosenchyma, in which the hexagonal sections of the cells interdigitate laterally and vertically respectively. The layer of soap bubbles over the bottom of the jar tends to impose a prosenchymal arrangement on the overlying strata. The patterns in Figure 6 and the conventional orthic 14-hedra in Figure 7 illustrate that position, characteristic of cells which increase in number by vertical division, enlarging the girth of the stem. If, however, Figure 7 is rotated clockwise 35°, the 14-hedra present hexagonal facets above and below, as is characteristic of parenchyma. They then have 2 tiers of lateral facets, variations in which have been expressed in a series of diagrams very different from those in Figure 6 (cf. Amer. Journ. Botany, 1943, *30*, p. 80). They show why the 14-hedron of formula 0–12–2, occurring in bubbles, has not been found and is not likely to be found in parenchymal cells. These cells increase chiefly by transverse division, and parenchymal orientation is characteristic of pith cells in elongating stems. The Kelvin 14-hedron, turned about, accounts for the shape of parenchymal and prosenchymal cells in their 3 dimensions.

The Kelvin 14-hedron exists in 2 varieties. Five years before he became Lord Kelvin, Sir William Thompson wrote[40]—"Given a model of the plane-faced isotropic tetrakaidecahedron, it is easy to construct approximately a model of the *minimal tetrakaidecahedron*. . . . No shading could show satisfactorily the delicate curvature of the hexagonal faces." That shape, with undulating hexagonal facets and plane quadrilaterals with out-curved sides, has less surface area than any other uniform shape into which space may be divided, and in so far deserves Kelvin's designation of "minimal 14-hedron"; yet the plane-faced non-stackable 14-hedron of formula 0–12–2 has distinctly less surface. Later Kelvin referred to the minimal *plane-faced stackable* form, in which the 6 quadrilateral facets are squares, as the "*orthic 14-hedron.*"

The determination of the curvature of the arcs in Kelvin's minimal 14-hedron, as he said, may be "easily carried to any degree of approximation that may be desired . . . though not worth the trouble." Accordingly its surface area has never been calculated. But, for the writer's benefit, Lifshitz[41] has shown that by substituting conical surfaces which resemble the Kelvin pattern, the reduction in surface area over that of an orthic 14-hedron of the same volume is "0.103 per cent." In a communication to the Nederlandsche Akademie Professor van Iterson[42] and, working under his direction, Meeuse in his doctor's thesis,[43] have shown that it is not the plane-faced orthic

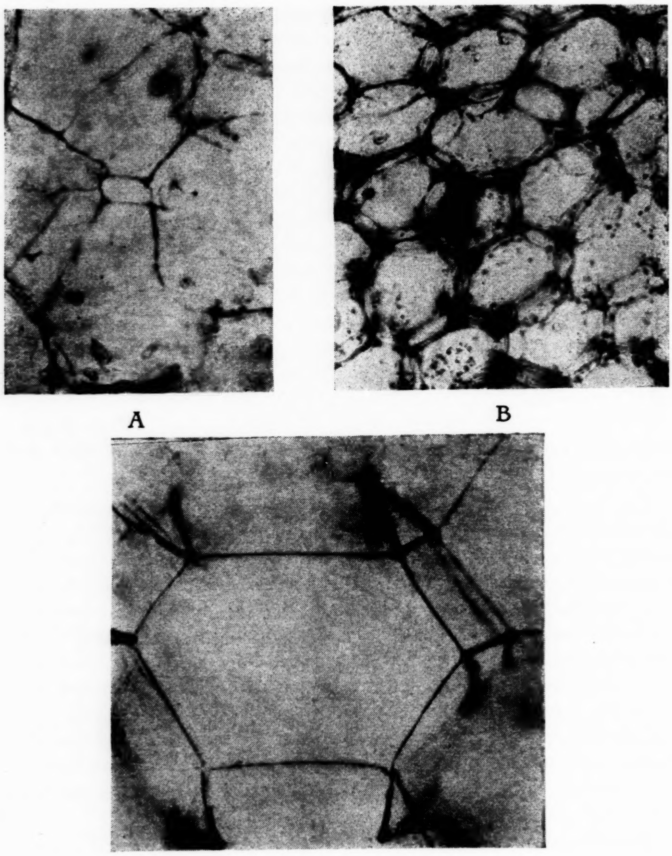


FIGURE 8. A. Quadrilateral facet suggesting the plane equilateral surfaces with slightly out-curved edges characteristic of Kelvin's minimal 14-hedron. Carrot, × 170. Fixed tissue, prepared and photographed by Prof. B. F. Lutman. B. Numerous quadrilateral facets of minimal form in the stem of a tomato plant. × 170. Photograph received from Prof. H. B. Reed, showing part of his Fig. 2, Amer. Jour. Bot., 33, 780, 1946. C. Facets of a parenchymal cell of *Asparagus sprengeri*, × 185. Prepared and photographed by Dr. A. D. J. Meeuse, included in Tab. III D of his Dissertation.[43]

14-hedron of Kelvin which cells approach, but rather its geometrical refinement, the "body of Thomson" or Kelvin's *minimal 14-hedron.*

Van Iterson reported that for 15 years he had demonstrated that "numerous cells approach the orthic 14-hedron" in the cortical parenchyma of the root-tubers of *Asparagus sprengeri*—"an object in which it may be recognized almost at once even by an unpractised microscopist." He realized the significance of Meeuse's observation that all 4 sides of the quadrilateral facets commonly show a slight outward curvature. Meeuse admits that "it does not matter as a rule" whether we consider Kelvin's minimal or his orthic 14-hedron to be "the fundamental shape of cells: the latter is simpler in structure and easier to work with." In several photographs, however (one being our Fig. 8C) he has shown the subtler features of the minimal 14-hedron. Now that attention has been called to the slightly curved outlines of the quadrilateral facets, they are frequently observed. Figure 8A is from a section of a carrot prepared by Prof. B. F. Lutman for another purpose: in 8B several may be seen in the stem of a tomato plant studied by Prof. H. S. Reed.

"It is not to be expected that the 'ideal' cell shape will often be perfectly realized . . . a perfect likeness has never been reported before" (Meeuse). To find how frequently such shapes occur in Asparagus and Rhoeo—two tissues especially recommended by van Iterson and Meeuse for their regularity—Hulbary made a statistical study of 100 cells of each.[44] He found 73 different combinations of facets, with only 2 cells of the 6–0–8 formula, and concluded that "no pattern stands out as one from which all others may be derived."

This conclusion is reaffirmed by Prof. Hulbary in his full publication in the November number of the Amer. Jour. Bot. (35, 558–566, 1948), distributed after the completion of the present paper, yet allowing the insertion of this paragraph as a postscript. Having found that 100 parenchymal cells in *Rhoeo*, with an average of 14.24 facets, included 18 14-hedra, 2 of which were of the formula 6–0–8, Hulbary studied 100 14-hedra in that tissue. Eleven of them were 6–0–8, which accords with his previous percentage. For that and other reasons, the parenchyma of *Rhoeo* appears to be the most regular thus far statistically tabulated. However, Hulbary finds that 47 per cent of its 14-hedra have the configuration 4–4–6, and states that "the reason for the recurrence of this pattern is not apparent." A possible reason is that the 4–4–6 combination is a group of diverse patterns, including a hexagonal prism with 2 facets on every lateral face, arranged as figured and described in the Amer. Scientist, 34, 366, 1946; also such a prism with one undivided lateral face, one with 3 tiers of facets, and the rest with 2 tiers, as figured by Hulbary for *Rhoeo;* or a pentagonal prism with 3 tiers of facets on 2 lateral faces and 2 tiers on the other 3; etc.;

whereas the meticulous 6–0–8 pattern, in a random elimination of the tetrahedral angles of a rhombic 12-hedron, would occur but once for 28 examples of the 4–4–6 (Reference 35). The irregular parenchyma of elder and *Eupatorium* sufficed for recognition of the typical 14-hedral shape, and whatever importance that type may have depends upon its application to all undifferentiated parenchyma. Hulbary, in *Ailanthus*, was the first to find the 6–0–8 combination in cells statistically studied (Amer. Jour. Bot., 31, 561–580, 1944); van Iterson and Meeuse have reported it in *Asparagus* with convincing photographs; Hulbary has now established statistically its occurrence in *Rhoeo.*

Bok,[45] in discussing bubbles without the benefit of Matzke's count that "more than five-sixths had 13, 14, or 15 contacts," argues that "froth chambers are approximations of regular dodecahedrons." Since at every corner in a foam each edge should meet 3 others at equal angles of approximately 109° 28′ 16″,[46] and in assembled *orthic* 14-hedra each edge meets 2 others at angles of 120° and the third at 90° (av. 110°), Bok rules out that shape as proposed through "a faulty trend of thought." He does not mention Kelvin's *minimal* 14-hedron, in which, through the curved edges observed by van Iterson and Meeuse, those angles approach the uniform angles of foam. With weaker surface tension and fewer pentagonal facets in cellular tissue, the approach to the Kelvin pattern is so manifest that that shape can confidently be accepted as a basis for many lines of further investigation. A reconstruction and volumetric study of the parenchymal cells in Eupatorium, arranged in their vertical columns, is sufficient ground for that expectation (Lewis[32]). The fundamental organization of the higher plants may then be indicated in a final diagram (Fig. 9).

Figure 9A is a vertical section of a column of 3 orthic 14-hedra surrounded peripherally by 26 portions of the same, 10 of which appear in the section. The simplest of these portions, as Dewar said of a similar arrangement of bubbles, are "pyramidal frustums, bounded externally by curved bubble films." The short shaft is encircled transversely by 2 layers of 9-hedra. It could be lengthened indefinitely by adding 14-hedra to the central column, with another layer of six 9-hedra for each addition. Over either end of the column there are 7 cells—an axial, apical cell surrounded by a circuit of 6 portions; and the total facets for all 7 are 50, whether the apical 14-hedron is sectioned through its lower, middle, or upper third, leaving it an 8-, 11- or 14-hedron respectively.

Figure 9B is a diagrammatic apical view of a larger shaft, in which 3 circuits of polyhedra surround the axial 8-hedral portion of an orthic 14-hedron. With modifications due to 2 schematic cell divi-

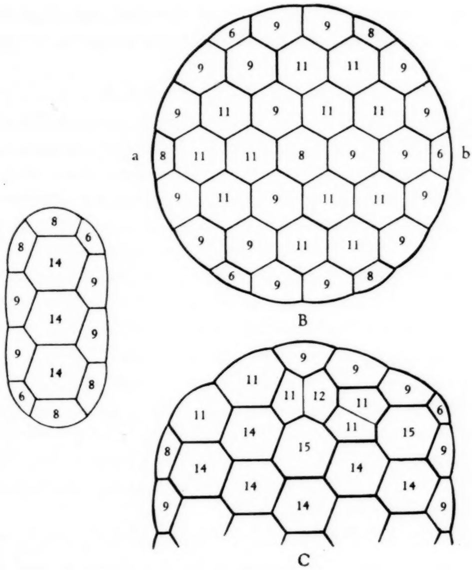


FIGURE 9. A. Median vertical section of a column of 3 orthic 14-hedra, enclosed in a layer of epidermal polyhedra which are portions of orthic 14-hedra. Numerals indicate the number of facets of each polyhedron. B and C. Two views of a similar but larger shaft, composed of 19 columns of parenchymal polyhedra, with the end of the entire shaft rounded to the extent shown in the median vertical section C. B is a diagrammatic surface view of the end of the shaft in C, with the number of facets of each polyhedron recorded. In C, 2 cell divisions have been introduced, converting the apical cell of B into the 9-hedron of C, and otherwise modifying the pattern.

sions, a vertical section of 9B, in the plane *a* to *b*, appears in 9C. At the apical surface in this simple scheme, it is seen that there is one sectioned 14-hedron at the summit of every vertical column. According to an old formula for finding the number of cells in honeycomb or kindred objects, when N is the number of circuits, the number of cells in a single transverse layer of the shaft (or in the surface view of the top, which is the same) is $3N(N+1)+1$. $6N$ is the number of epidermal cells in a cross section of the shaft, and $6(11N-2)$ is their number of facets: $3(N^2-N)+1$ is the number of parenchymal cells in such a cross section, and they all have 14 facets. These numbers,

of course, may become averages, and the deduction of 12 facets in the epidermal layer may be transferred, in whole or in part, to the parenchyma.

Over the end of a shaft composed of 14-hedra, there is a further reduction of facets than occurs in the layers around the sides of the shaft. The numerals in Figure 9B indicate the number of facets of the polyhedra covering the rounded end of that shaft with 3 circuits, the sum of which is expressed in the general formula $33N^2 + 15N + 2$. The same number of facets (344) would occur in the flat end of a similar shaft cut out from an integrated mass of orthic 14-hedra, provided that the sharp cut edge at the junction of the horizontal and vertical sides of the cylinder was eliminated—it would not be there in bubbles or in liquid bodies (cf. Lewis,[32] p. 628).

The external mosaic covering the shaft and its ends consists entirely of hexagons except for the required loss of precisely 12 sides. In Figure 9B the loss is located in 3 cells which have quadrilateral facets externally; they would be matched by 3 others at the opposite end of the shaft. These 3 are 6-hedral cells (one at *b*). The peripheral 8-hedral cells in 9B (one at *a*) present hexagons externally, like the 8-hedral cells in Figure 9A.

In Figure 9C, the 2 hypothetical divisions which have been added are enough to suggest a meristem with dermatogen and plerome—a corpus and tunica. A vertical division of an axial orthic 14-hedron, in the midst of others like it, produces a pair of 11-hedra (formula 4–4–3), thereby introducing 20 pentagonal facets, 12 of which are formed on 4 adjacent cells. This may readily be visualized from the mutual relations of an entire and a bisected conventional model of either the orthic or minimal type. The 4–4–3 is a common facet combination, with 5 records in 50 small cells (Marvin[47]), one of them being, as in Figure 9C, half of a 14-hedron, vertically sectioned.[48] This division, in the figure, makes the underlying body a 15-hedron (5–3–6–1), matched by 3 cells in 150 (Hulbary), and it produces an epidermal 4–4–1, of which combination Matzke counted 11 in 200 epidermal cells of Aloe.

It is not to be supposed that cells occur as masses of 14-hedra to be disarranged by the subsequent introduction of division, as in a diagram, since the initial clusters arise by division, with its effects there from the outset. Nevertheless it appears that a typical geometric form for cells has been established, through Kelvin's mathematics, as a first step toward placing plant and animal cytology on an adequate geometrical basis. If his type forms are accepted as the source of

scores of deviations—in part random deviations—the way is open for profitable consideration of many unsolved morphological problems.

Summary and Conclusion

An attempt has been made to present the simplest possible arrangement of undifferentiated cells and their intercellular spaces preliminary to studying the evolution of complex cell patterns. The shape of primitive cells in masses appears to depend on 5 paramount factors.

(1) *Geometric necessity.*—This is the bond whereby, in space-filling aggregations, bodies of equal size have been found to have an average of approximately 14 facets, whether they are cells, solids or bubbles. If a uniform shape is assumed they become regular 14-hedra. Geometrically it is impossible for them to be 15- or 13-hedra. Although the average of 14 is realized for bodies promiscuously assembled, special arrangements may reduce the facet number. Notably when equal spheres are stacked in cannon ball fashion before compression, they yield 12-hedra, each with 6 tetrahedral angles, at each of which 6 bodies should meet at a mathematical point. Failing to fulfill this exacting requirement leads toward the 14-hedral shape. Inherently a mass of 14-hedra must be enclosed in a surface layer, epidermal or epithelial, in which a single contact with the surrounding medium is substituted for contacts with 4 surrounding polyhedra. These 11-hedral peripheral cells have the form of bisected central 14-hedra. Yet a shaft formed of columns of 14-hedra cannot be covered by a layer of 11-hedra without a deduction of 12 facets in every transverse stratum. In accordance with Euler's law, the possible combinations of facets, corners and edges of any cell and of every mass of cells are geometrically determined.

(2) *Surface tension* and other forces resulting in minimal surface.—"This does not enter into the formation of compressed plastic spheres" (R. J. Piersol[49]). In liquid films tetrahedral angles are unstable, and their elimination leaves only the 14-hedron as the uniform space-filling possibility for bubbles and cells of least surface. With bubbles surface tension is sufficient to produce examples of all the unstackable combinations of 12, 14, 15 and 16 facets which, if isolated and regular, would have the least surface for their volume (Goldberg). Correlated with low surface tension, none of these shapes have as yet been found among cells. The downward deviation of the average number of facets of bubbles in unarranged foam to 13.70, as reported by Matzke, is unaccounted for; but his finding that the central bubbles, in a dish lined with those averaging 11 facets, show slightly higher average facets when their volume is 1/20 cc. than when their volume

is 1/10 cc. (13.74 facets as compared with 13.69) is a trend which accords with the geometrical expectation. It appears improbable that irregular aggregates have less surface area than Kelvin's mathematical minimal pattern.

(3) *Cell division.*—This process, perhaps electro-chemical, is opposed to surface tension, since it increases the cellular surface. It need not change the average number of facets of the cell mass in which it occurs, but it introduces an abundance of pentagonal facets in any group of Kelvin 14-hedra, which otherwise could lack them altogether. Since divisions tend to be in a predominant plane, which would be transverse in stems increasing in length, and vertical in those increasing in girth, they cause the cells to be arranged in vertical parenchymal columns, or in transverse prosenchymal layers, respectively, as is essential for producing a mass of Kelvin 14-hedra.

(4) *Turgor.*—Also opposed to the contractile effect of surface forces is the expansion from turgor and growth whereby many cells cease to be isodiametric, and actively or passively become drawn out into elongate or stellate forms. Even though tall epidermal cells may become globular when isolated, they should not be regarded as spheres which by expansion have filled out their interstices, like peas in Buffon's experiment. Yet swollen peas often yield cell-like combinations of facets.

(5) *Organization.*—This is the elusive factor which Schleiden recognized as "paramount" more than a century ago, whereby growth and division are so controlled as to produce filaments, fibers, membranes or compact masses as may be proper for the organism. Fibers, as elongated 14-hedra, would be rendered short and inefficient by a few successive transverse divisions. In another century something more should be known regarding the nature of the "organizer," which coordinates the foregoing factors.

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